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Species climatic niche explains drought-induced die-off in a Mediterranean woody community

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Abstract. During the last decades, plant die-off has been reported worldwide as a result of increased frequency and intensity of extreme drought events. From a niche perspective, a species performance should decrease as the climatic conditions defining a drought event differ from those characterizing the species climatic niche (the average conditions experienced by the species). Species distribution models (SDMs) can potentially be used to test the link between species performance and their climatic niche by means of climatic suitability indexes. We studied the remaining green canopy of 18 woody species co-occurring in a Mediterranean shrubland from the central Iberian Peninsula that experienced a severe die-off following an extreme drought event. We found that the suitability of the climatic conditions estimated by SDMs strongly declined for all species during the extreme drought event. Species die-off was significantly explained by the decrease in climatic suitability during the event, estimated as the ratio between the historic and the extreme event climatic suitability. Species with high occupancy levels across the landscape exhibited higher die-off likely because (1) these species have short life-span and mortality would be compensated by later high recruitment or (2) populations of rare species may have experienced local adaptation to drier conditions. Our results indicate that extreme drought events can have a negative effect, even in shrubland communities living in arid environments. Also, we develop a new approach that connects population-level responses to species climatic niches through SDMs, and it can be applied to predict community responses to strong climatic variability, such as drought events.

Key words: climatic niche; correlative niche models; defoliation; die-off; drought responses; extreme drought event; Maxent; Mediterranean ecosystems; niche-based models; shrubland; species distribution models.

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INTRODUCTION

Climate change is increasing the intensity, frequency, and length of droughts through increased temperatures and reduced precipitation across many regions of the globe (IPCC 2013). As a result, many of these regions are experiencing increased aridity (D'Odorico et al. 2013) and extreme drought events, leading to tree and shrub die-off episodes worldwide (Allen et al. 2010, Greenwood et al. 2017). These events trigger changes in community structure and composition that may promote new communities with different ecological characteristics (Lloret et al. 2012). Ultimately, the extent to which ecosystem features change as a result of drought events depends on species' performance under drought (e.g., die-off).

Species' performance under drought can be tied to niche theory through the concept of fundamental niche proposed by Hutchinson (1957). The fundamental niche of a species is a multidimensional

space defined by abiotic factors determining species occurrence. Thus, the fundamental niche explains species frequency and abundance across their geographic distribution, along with dispersal, competitive ability, and biotic interactions (Pearson and Dawson 2003). The climatic conditions that species experience during extreme drought events are likely close to the edge of their climatic niche space relative to average climatic records. Therefore, under such extremely dry conditions, we can assess how the performance of populations of coexisting species reflects the climatic components of their fundamental niche, which we call the "climatic niche."

Species distribution models (SDMs), also known as correlative ecological niche models or climatic niche models, estimate a statistical relationship between the geographic occurrence of a species and the environmental and/or spatial characteristics—climate—of the sites where it is present (Franklin 2010). Thus, SDMs can use climatic variables to describe the climatic space (i.e., the climate conditions that determine the center and the edge of the species climatic niche) where a species is currently present, and to estimate how extreme are the climatic conditions experienced by a particular population relative to its climatic niche at a given time. Therefore, SDMs provide an estimation of the climatic suitability of a location for a given species. This is performed by an algorithm that relates records of presence of a species to the climate conditions at a given locality. This climatic suitability is calculated from the climate conditions of a given period of time; particularly, it can be calculated for the period when extreme drought events occur. This short-term application of SDMs to describe local population performance merits exploration because SDMs are not only defined by climate and it is not yet clear how applicable SDM outputs are to describe the performance of a given population over large spatial extents (VanDerWal et al. 2009, Thuiller et al. 2014). Here, we use SDMs to investigate whether changes in the climatic suitability for different coexisting species associated with extreme climatic drought correlate with local species responses (i.e., loss of green canopy).

We focus our study in a Mediterranean community located in the northeastern Iberian Peninsula, where species exhibit physiological mechanisms and morphological characteristics that provide them with certain degree of resistance to drought (Bussotti et al. 2014, Trifilo et al. 2014). Thus, populations of species with high climatic suitability under Mediterranean climate are expected to exhibit less die-off under extreme drought events than those of species with low climatic suitability because the latter are expected to have higher moisture requirements. Nevertheless, typical Mediterranean species can still be severely damaged if the intensity and/or length of a drought period substantially surpasses what has been historically experienced (Lloret et al. 2016, Venturas et al. 2016). Assessing the vulnerability of Mediterranean communities to extreme drought is especially relevant since the climatic conditions experienced under these extreme events can be similar to those predicted to be standard in the future (IPCC 2013). These predicted conditions correspond to high aridity and eventual loss of vegetation cover, which will be particularly threatening in the study area given that it is located at the boundary between Mediterranean and semiarid regions.

Comparing species responses within the community, we hypothesized that (1) species historically experiencing conditions closer to their climatic niche center show greater resistance to the extreme drought event, estimated as mean percentage of green canopy of individuals relative to the green canopy present in healthy plants; and (2) species experiencing a greater reduction in climatic suitability during the drought event relative to their historic record exhibit higher die-off. We further explored the relationship between resistance to the extreme drought event and species local abundance testing whether (3) more abundant species (i.e., higher frequency of occurrence across the territory or higher local population density) would show greater resistance to drought-induced die-off. We base this hypothesis under the general assumption that more abundant species would be those that are more successful under the arid conditions of Mediterranean climates.

Materials and Methods

Study area

The study site was located in the Monegros countryside, in the central Ebro Valley of the northeast Iberian Peninsula (41°25′ N, 0°4′ E), at

~280 m above sea level. Ten sampling sites were established evenly distributed in a 10-km^2 grid in the center of the Barranco de Valcuerna Basin (Fig. 1). All sites were located in areas at least 30 m away from any trail that could generate a boundary effect. Additionally, all sites were located in areas of similar orography to ensure that they were comparable.

This area has a Mediterranean climate with a semi-arid tendency (Fig. 2a). Mean annual precipitation is about 390 mm with seasonal variability causing chronic summer droughts. Spring and autumn precipitation represent 30% and 32% of annual precipitation, respectively, while winter and summer precipitation represent 18% and 20% of the annual precipitation, respectively. Mean annual temperature is 14.8°C with high seasonal variation: from 6.1°C of mean temperature in the coldest month (January) to 23.8°C in the hottest month (July). For the period 1950–2000, the mean seasonal extreme values of temperature were 2.9°C in winter and 29.8°C in summer (Fig. 2a). In recent decades, this area has experienced a trend toward increased aridity followed by a drought event during the period 2005–2013, becoming extreme in 2006–2010, see next section, that has resulted in decreased vegetation cover, as detected by remote sensing (Pueyo and Alados 2007, Vicente-Serrano et al. 2012). At the population level, this recent drought has triggered widespread defoliation and plant mortality (see Appendix S1).

The studied sampling sites correspond to an open continental–Mediterranean shrubland (*Rhamneto–Cocciferetum pistacietosum*) association (Braun-Blanquet and Bolòs 1957) with occasional occurrence of trees (*Pinus halepensis* Mill. and *Juniperus phoenicea* L.). Dominant shrubs were *Rosmarinus officinalis* L., *Rhamnus lycioides* L., *Helianthemum syriacum* (Jacq.) Dum. Cours., *Cistus clusii* Dunal, *Quercus coccifera* L., and *Genista scorpius* (L.) DC. (Braun-Blanquet and Bolòs 1957). These species typically have a Mediterranean distribution, although some of them, such as *J. phoenicea* L. and *Q. coccifera* L., are at the edge of their geographic distribution in this area. This vegetation develops on leptosols over marls and limestones that are rich in gypsum.

Description of the extreme drought event

We performed an analysis of the variability of the climate over the last 63 yr by calculating the distributions of seasonal precipitation and

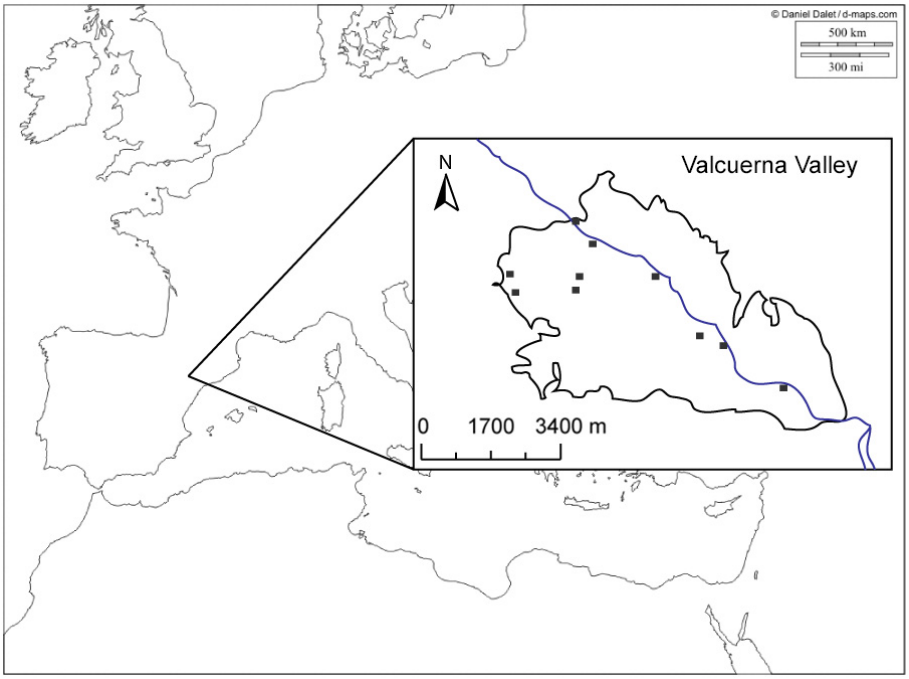

Fig. 1. Map of the study area and sampling site locations. Gray squares indicate sampling sites.

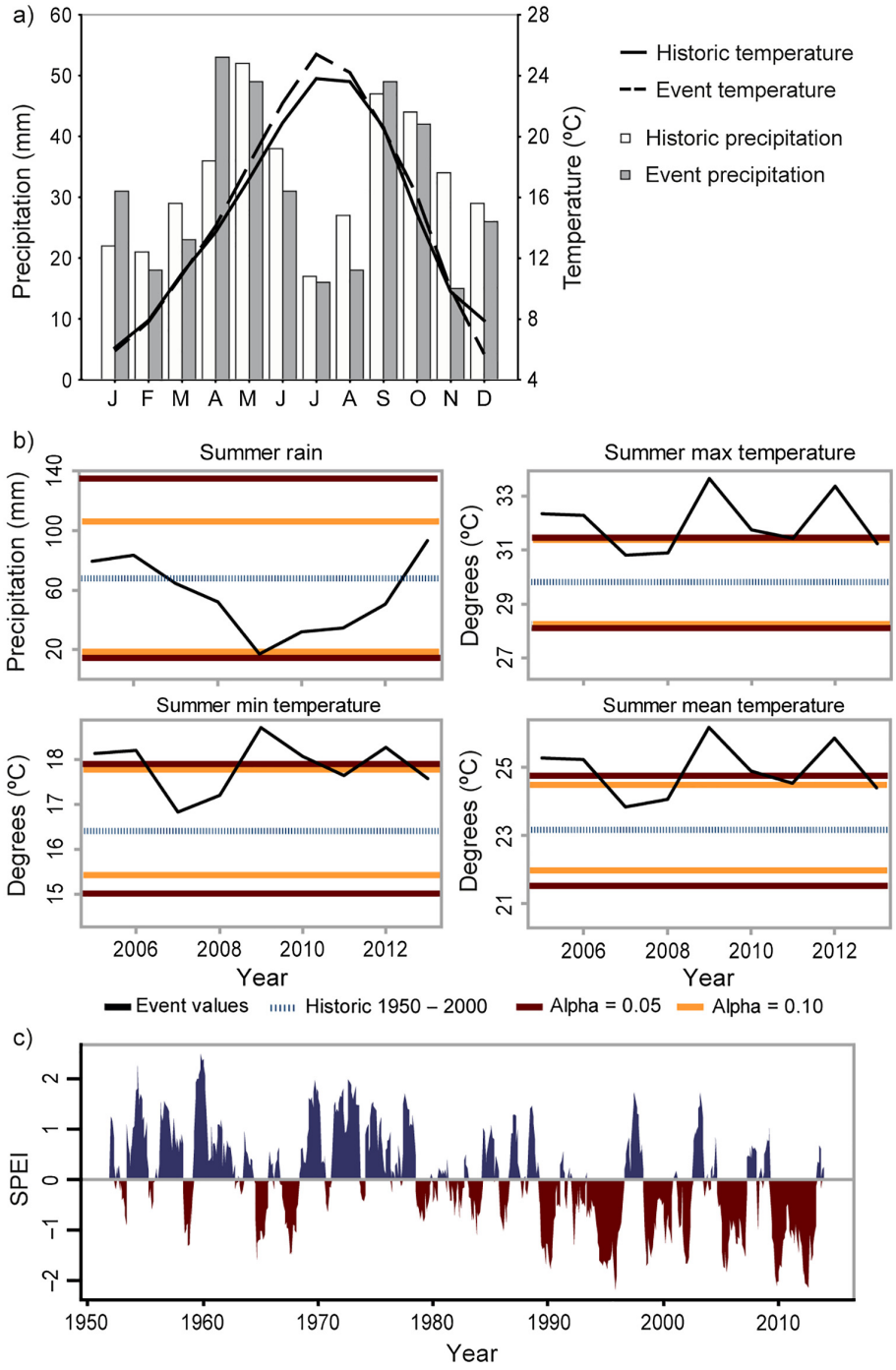

Fig. 2. Climograph of the study area and analysis of the extreme drought event. (a) Monthly precipitation (bars) and temperature (lines) during the period 1950–2000 (Historic) and the period 2006–2010 (extreme drought event). (b) Summer values of precipitation, maximum temperature, minimum temperature, and mean temperature from years 2005 to 2013. Red and orange lines show significant (5th percentile) and marginally significant (10th percentile) alpha values, respectively, considering the estimated probability distribution of values for these variables during the period 1950–2000. Dotted lines show average (50th percentile) values based on the period 1950–2000. Significance is achieved when 5th percentile of the probability distribution is exceeded.

(*Fig. 2. Continued*)
(c) Standardized Precipitation-Evapotranspiration Index (SPEI) from years 1951 to 2013. Red colors indicate water deficit (i.e., drought periods), while blue colors indicate water surplus. Each SPEI value is calculated using the data of the last 12 months. Data correspond to the locality Zaragoza Airport, sited at 80 km west of the Valcuerna study site. Source: Agencia Española de Meteorología (AEMET), Ministerio de Agricultura, Alimentación y Medio Ambiente, Gobierno de España.

maximum, minimum, and mean temperatures for the historic period of 1950–2000 (location: Zaragoza Airport, 80 km from study area); source: Agencia Española de Meteorología (AEMET). We also calculated the Standardized Precipitation-Evapotranspiration Index (SPEI), a drought index that integrates the coupled effects of temperature and precipitation showing negative values under drought and positive values under water surplus (Vicente-Serrano et al. 2010). A year would be considered "extreme" when the seasonal temperature or precipitation fell beyond the 10th percentile of the respective distribution of the historic period (1950–2000). Applying this method for the drought event (2005–2013), extreme summer temperatures were detected throughout the entire period. Temperatures increased during the extreme drought and corresponded to the most extreme 5% of values found in the last 60 yr (Fig. 2b). Precipitation was also particularly low in summer 2009, after decreasing for three consecutive years and reaching minimum values that fell beyond the 10th percentile. The patterns observed from temperature and precipitation separately were confirmed by the SPEI calculated for the period 1951–2013. While the SPEI detected a minor water surplus between 2007 and 2008 (Fig. 2c), temperatures were already extreme in 2006 and precipitation was strongly declining since that year—below the historic average in 2007 and following years (Fig. 2b)—indicating the beginning of the extreme drought event. For this reason, we decided to include 2007 and 2008 as part of the extreme drought period to ensure that we were not missing the beginning of the event and to include potential delayed effects resulting from the 2006 drought. Therefore, the extreme drought event was defined as the period of 2006–2010.

Field sampling criteria

In each of the 10 sampling sites, a 50 × 50 m stand homogeneously covered by shrubland was chosen. Adults from 20 woody species were surveyed in June 2013 according to the following criteria: (1) species that comprise a wide range of life forms, from small shrubs (chamaephytes) such as *Helianthemum* sp. pl. to small trees (nanophanerophytes) such as *J. phoenicea* (Appendix S2), (2) species that allow reliable visual estimation of drought-induced defoliation, (3) species covering a range of abundance and frequencies within the study area.

Estimation of demographic variables

Since the size of the stands was too big to count all individuals belonging to each species, species stand density (hereafter stand density) was estimated following a nearest neighbor procedure (Kent 2011). In each stand, a total of 20 points were randomly established. The distance from each point to the nearest plant of each studied species present in the stand was then measured. Plants outside the stands but within 5 m of their limits were included in the nearest neighbor measurements to avoid overestimating nearest neighbor distances at points located close to the stand edge. For each species, the average distance to the nearest plant was used to calculate the minimum circular area needed to find the species within the stand. Then, the stand density of a given species was estimated as individuals per stand by dividing the area of the stand by the area needed to find an individual of a given species.

Since this method could underestimate rare species within large stands (i.e., they may be less detectable), a more accurate method was used for species with low abundance. For species with <20 adult individuals growing within the stand, stand density was estimated by counting all individuals present along two perpendicular transects located in the center of the stand. Transects were 1 × 50 m for small-sized species (<20 cm high) and 2 × 50 m for medium-sized species (20–50 cm high). This method was not used as the general approach because it can potentially

bias the abundance of species that have a clumped distribution within the stand. In that sense, the nearest neighbor procedure is more desirable given that it establishes random points across the whole stand ensuring a more homogeneous sampling effort. Both methods used to estimate species stand density revealed consistency after correlating the measures obtained by nearest neighbor distances and by transects in the same stand for 18 species ($R^2 = 0.72$, $P < 0.001$).

Species' population density and frequency of occurrence were then estimated across the valley. Species' population density (hereafter local density) was calculated by averaging the values of stand density for all the stands, including stands where the species was not found (Appendix S3). Species frequency of occurrence across the valley (hereafter species frequency) was calculated as the number of stands in which a species was found (ranging between 1 and 10). Species frequency is a coarser measure of the abundance than local density, but it represents a more robust estimation of species occurrence at the landscape level since it is not affected by fluctuations of abundance at the stand level due to microclimatic variation (Appendix S3).

The size of the studied species was also measured to account for potential effects of plant size on green canopy levels. Larger plants are expected to have access to larger pools of resources like water or nitrogen and have larger carbon storages than smaller plants, allowing longer green canopy persistence following drought. The size of the studied species (hereafter species volume) at each stand was estimated by averaging the volume of 15 adult plants randomly selected within the stands where they were present. Volume was calculated by multiplying the height of the plant by the ellipsoidal area of the canopy (defined by two perpendicular diameters crossing the center of the plant). Volume was used rather than plant height or diameter separately because it is a more representative measure of the species size (i.e., biomass).

Estimation of green canopy levels

Green canopy levels were visually estimated as a proxy for the species response to drought (die-off) as the percentage of green leaves present relative to the amount in healthy individuals found in the study area. This method is standard for estimations of drought-induced die-off in ecosystems dominated by woody vegetation (Carnicer et al. 2011, Galiano et al. 2011, Nakajima et al. 2011, Boehmer et al. 2013) and has also been used to categorize forest health across Europe by the International Cooperative Program Forest Inventory (Eichhorn et al. 2016). Green canopy levels were measured in the canopies of the plants that were used to estimate stand density (Appendix S3), but only species with at least 20 individuals within the stand were considered at each site to reduce stochasticity in the estimation of green canopy levels at stand level. Only plants that were recently defoliated, approximately within the past year, were surveyed. Individuals were categorized as recently defoliated only if the tips of their branches were still present and the defoliated leaves were found in the ground under their canopy. Thus, we avoided individuals with signs of old decay (stumps, decomposing stems, branches without thin tips or buds). Although we considered recent defoliation, woody vegetation often shows lagged responses to climatic variability (Lloret et al. 2004); thus, our measures still reflect the chronic drought that the region has been experiencing since 2009, as shown by SPEI (Fig. 2c).

Additionally, species-specific correlations between visual estimations of green canopy and actual amounts of present green leaves (leaf-to-branch weight ratio) were previously calculated to ensure that visual estimations were reliable. For nine of the studied species, representative of the full range of life forms and several families, 40 individuals showing the full range of green canopy levels (i.e., from 0% to 100%) were sampled across the study area. For each individual, green canopy levels were assessed visually and three branches of a given diameter (determined beforehand for each species) were randomly collected, dried, and weighed to obtain whole branch dry weight and remaining green leaf dry weight. The actual green canopy levels were calculated as the ratio between green leaf dry weight and whole branch dry weight (including leaves). These values were standardized for each species by dividing the actual green canopy levels of each individual by the highest value found within the same species to obtain percentages of green canopy that were comparable across species (see Appendix S4 for more detailed methods). Finally, visual estimations and standardized actual green canopy levels were

correlated for each species. We also build these same correlations using non-standardized actual green canopy levels to ensure that the correlation was already present at that point and to demonstrate that standardizing values made canopy levels comparable between species (see Appendix S4: Tables S1, S2, and Fig. S1). As expected, the correlations were found in both standardized and non-standardized data for each species. Also, standardizing increased both the degree of correlation between visual and actual canopy values across species and the degree of overlap between species-specific correlations, thus indicating that different species showed similar ranges of actual canopy values after standardizing by the healthiest individuals (see Appendix S1 for pictures of healthy plants). On average, visual estimations explained ~60% of the variability existing in standardized actual green canopy levels across species, thus ensuring that visual estimations were reliable. Additionally, the correlations clearly indicated that our visual estimations were able to distinguish healthy individuals from defoliated ones and the gradient of defoliation stages present between these two despite the existing variation (see Appendix S4 for more detailed methods and results). No significant activity of browsers of any kind that could potentially affect green canopy values was observed in our stands for any species.

Climatic suitability models and Climatic Drought Index (CDI)

Changes in climatic suitability between historic (1950–2000) and extreme drought events (five years, 2006–2010) were estimated using SDMs. We built SDMs using the presence-only Maxent algorithm (Elith et al. 2006, Phillips et al. 2006). The output of the SDM is also called suitability and is calculated using the climatic conditions where the species occur (using presence data records) against the climatic conditions of a delimited extent (background). The output is thus a relative occurrence rate and describes "the relative probability that a given cell is contained in a collection of presence samples" (Merow et al. 2013). Then, this relative probability is transformed to a probability ranging from 0 to 1 using a logistic transformation (e.g., logistic output; Merow et al. 2013). The SDM built under historic conditions was then projected to conditions under drought.

Presence records for each species were obtained from the Global Biodiversity Information Facility data portal (data.gbif.org) and subsequently filtered by deleting records without accurate information regarding taxonomic identification or location (Marcer et al. 2012). These presence records are unique for each species' and are used to model species' specific ecological niches. Background area should represent a geographical space that is currently available for colonization or has been colonized in the past by the modeled species (Barve et al. 2011). We used a latitude/longitude-bound box of presences to account for north–south variation in latitude through the glacial period.

Climate variables were chosen from the WorldClim database for the historic period (Hijmans et al. 2005) and from the AEMET database for the extreme event period. Spatial scaling was performed to match the spatial resolution of both SDMs (10 km). We selected 14 climatic variables from WorldClim representing both average and extreme conditions; both type of variables are recognized as important to describe species distributions (Zimmermann et al. 2009, see full list in Appendix S5).

We used Maxent default options of "automatic" feature selection and logistic output. We assessed models' accuracy using the area under the curve (AUC) on a randomly set aside 25% of the occurrences. In addition, we controlled for model extrapolation using the multivariate environmental similarity surface analyses (Elith et al. 2010).

For each sampling site and species, a measure of historic and extreme drought event climatic suitability was obtained. These values were averaged, respectively, for the entire study area of Valcuerna Valley. We used the ratio between historic and extreme event climatic suitability (CDI) as an index to measure the impact of the extreme drought event for each species (see Appendix S6 for details). The CDI assesses the degree of change in climatic suitability experienced by a species in a given locality due to the extreme drought event. High CDI values indicate large deviations of the climatic conditions relative to the conditions historically experienced by the populations at a given site, which reflects the relative position within their climatic niche space (see CDI values for each species in Appendix S3).

Statistical analyses

To assess the relationship between green canopy levels, climatic suitability, and species local abundance, we performed a general linear model (GLM; Mardia et al. 1979) with a normal probability distribution and a log-link function with green canopy levels as the dependent variable and historic climatic suitability, local density, species frequency, and species volume as explanatory variables. Species volume was also included to account for potential effects of plant size in green canopy.

Similarly, to assess the relationship between species green canopy levels and the degree of change on climatic suitability for the species during the extreme drought event, we performed a GLM with a normal probability distribution and a log-link function with green canopy levels as dependent variable and CDI, species frequency, and species volume as explanatory variables.

In all models, the non-significant variables were dropped to simplify the models and the Akaike information criterion (AIC) was used to ensure that simplified models performed as well or better than the full models (see Table 1). The GLM assessing green canopy levels in relation to local abundance performed better when using only species frequency as explanatory variable rather than using both species frequency and local density or local density alone. Thus, local density was excluded from the final model used to assess green canopy levels in relation to climatic suitability and local abundance.

Species that showed potential sampling errors and high outlier Cook's distances were removed from analyses. *Helianthemum apenninum* was excluded from all analyses, as it was difficult to distinguish in the field from *Helianthemum hirtum*. *Ononis tridentata* was excluded due to high Cook's distance from the GLM describing green canopy levels in relation to the historic climatic suitability and species frequency and from the GLM describing green canopy levels in relation to CDI and species frequency.

Additionally, phylogenetic generalized least-squares analyses were performed to ensure that phylogenetic relationships between species did not explain the observed patterns on green canopy levels (Appendix S7). Also, the variation in soil gypsum content was surveyed and analyzed but it did not show significant effects on green canopy levels or local density (Appendix S8).

All GLMs were performed using R software (version 3.1; R Foundation for Statistical Computing,

Table 1. Results of full and simplified models.

Model and factors	Model type	Estimate	95% CI estimates		*P*-value	df (full)	df (res.)	AIC
			2.5%	97.5%				
Green canopy level = Historic climatic suitability + Species frequency + Species volume	GLM				—	16	13	128.86
Intercept		4.579	4.321	4.808	***			
Historic climatic suitability		−0.309	−0.656	0.079	0.124			
Species frequency		−0.032	−0.057	−0.009	*			
Species volume		−0.036	−0.080	0.000	0.105			
Green canopy level = CDI + Species frequency + Species volume	GLM				—	16	13	127.83
Intercept		4.465	4.310	4.618	***			
CDI		−0.004	−0.008	0.000	0.095			
Species frequency		−0.034	−0.058	−0.009	*			
Species volume		−0.016	−0.062	0.024	0.482			
Green canopy level = CDI + Species frequency	GLM				—	16	14	126.54
Intercept		4.464	4.314	4.610	***			
CDI		−0.005	−0.008	−0.001	*			
Species frequency		−0.033	−0.058	−0.009	*			

Notes: AIC, Akaike information criterion; GLM, general linear model. Relationships between green canopy level and climatic suitability, and green canopy level and Climatic Drought Index (CDI, see text and Appendix S6) during the extreme drought event. Species frequency and species volume were also included as explanatory variables. The full models and their simplified models, statistical approach used, estimates with their confidence intervals (CI), *P*-values, degrees of freedom (df), and AICs are shown for each model. Simplified models are only shown when their AIC was lower than the full models. Significant *P*-values are indicated with asterisks (* < 0.05, ** < 0.01, *** < 0.001).

Vienna, Austria). R packages were also used to construct SDM layers (dismo, rgdal, raster), detect the extreme drought event (SPEI), and perform phylogenetic analyses (phylotools, ape, caper; see Appendix S11 for package citations).

Results

Our SDMs were accurate, with AUC values of at least 0.9 except for *Lithospermum fruticosum* (AUC = 0.538), which was excluded from subsequent analyses (Appendix S2). Multivariate environmental similarity surface analyses indicated that the extrapolation levels of our SDMs were fairly low with values over 20 for all species (Appendix S2).

We found clear evidence for all studied species of low climatic suitability during the extreme drought period 2006–2010 relative to the historic period 1950–2000 (Fig. 3; Appendix S9). This result is consistent with the changes in precipitation and temperature recorded during the extreme drought period in the studied region (Fig. 2).

The GLM used to analyze green canopy levels in relation to historic climatic suitability, species frequency, and species volume was significant ($P < 0.001$; Table 1). The effect sizes showed that only species frequency was significant ($P = 0.021$) and negatively related to green canopy levels. Frequent species appeared to be more impacted by the extreme drought event than less common ones (Fig. 4). The model was not further simplified because doing so rendered higher AIC values than the full model.

The GLM used to analyze green canopy levels in relation to CDI, species frequency, and species volume was significant ($P < 0.001$; Table 1). The effect sizes showed that both CDI and species frequency were significant ($P = 0.035$ and $P = 0.016$, respectively). Climatic Drought Index negatively influenced green canopy levels following a negative logarithmic-type function. This relationship indicates that species more impacted by the extreme drought event, in terms of remaining green leaves, proportionally experienced larger reductions in their climatic suitability (Fig. 5). Green canopy levels and species frequency showed a negative relationship.

Discussion

Our results demonstrate the link between local-scale processes, such as drought-induced population die-off during extreme climatic events, and the species climatic niche estimated from distribution patterns at a biogeographic scale. This link is

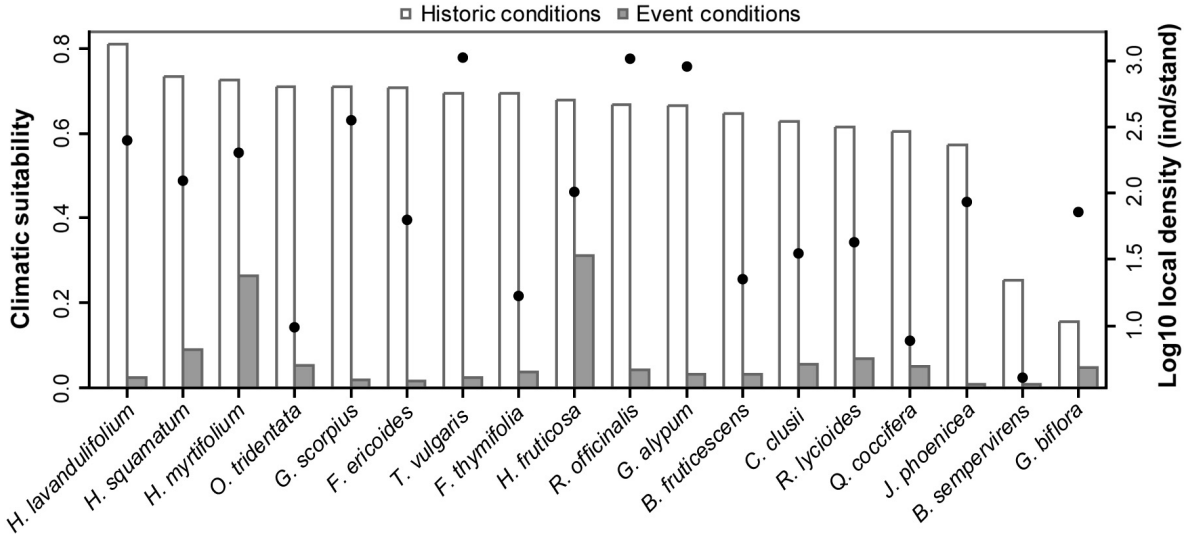

Fig. 3. Climatic suitability and local density of each species. Historic climatic conditions represent the period 1950–2000. Extreme drought event climatic conditions represent the period 2006–2010. Estimated local densities are represented as dots for each species (see Appendix S10 for densities with error bars). Local density values are logarithmically presented.

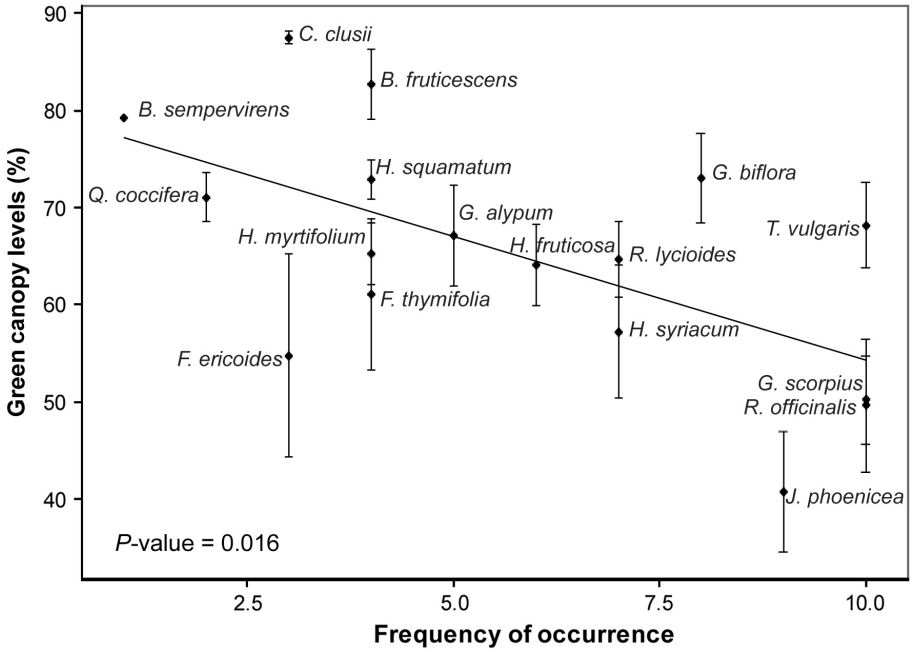

Fig. 4. Relationship between green canopy levels and species frequency. Frequency of occurrence represents the abundance of a species across all sampling sites. Error bars represent standard errors.

illustrated by the relationship between green canopy levels and changes in climate suitability during extreme climatic events (i.e., CDI), as we hypothesized. This relationship followed a negative logarithmic function, which indicates that the degree of canopy loss per unit of CDI is larger under small climatic suitability displacements. This non-linear relationship could be indicating a CDI threshold at which species start to experience stress leading to quick reductions in green canopy levels (Pook 1985). Beyond that threshold, plants only keep the minimum green canopy needed to maintain vegetative tissues alive while avoiding water loss (McDowell 2011). This pattern is strong enough to arise even in the presence of other factors such as microclimate variation between and within sites, variability in species and individual physiology, and the inherent sampling error of green canopy-level estimates. The latter one includes two potential cases: (1) Individuals categorized as healthy could poorly represent actual healthy plants if all individuals in the area have experienced certain degree of drought-induced defoliation and (2) green canopy levels of a species could be overestimated if an individual that accurately represents a healthy canopy is not found for that species. In the first case, our healthy individuals did not show any signs of defoliation (see Appendix S1 for examples), thus ensuring that they were good representatives of healthy plants. Additionally, even certain degree of defoliation in healthy plants would not have had a significant effect in our results since the severely defoliated plants were so easily discernible (see Appendix S1 for examples). In the second case, the healthy individuals used as a reference for visual green canopy estimations were determined across the whole study area rather than at the stand level. This ensured good coverage of the existing variability in green canopy levels and gave robustness to our measurements. Also, species that are known to shed leaves under drought stress, such as *Rhamnus lycioides*, did not exhibit larger variation in their green canopy levels compared to other species nor drive the relationship between green canopy levels and CDI. Consequently, the logarithmic relationship found between green canopy levels and CDI seems ecologically meaningful and not driven by a few species with particular responses. However, we do not discard the possibility that defoliation and CDI could follow different types of negative

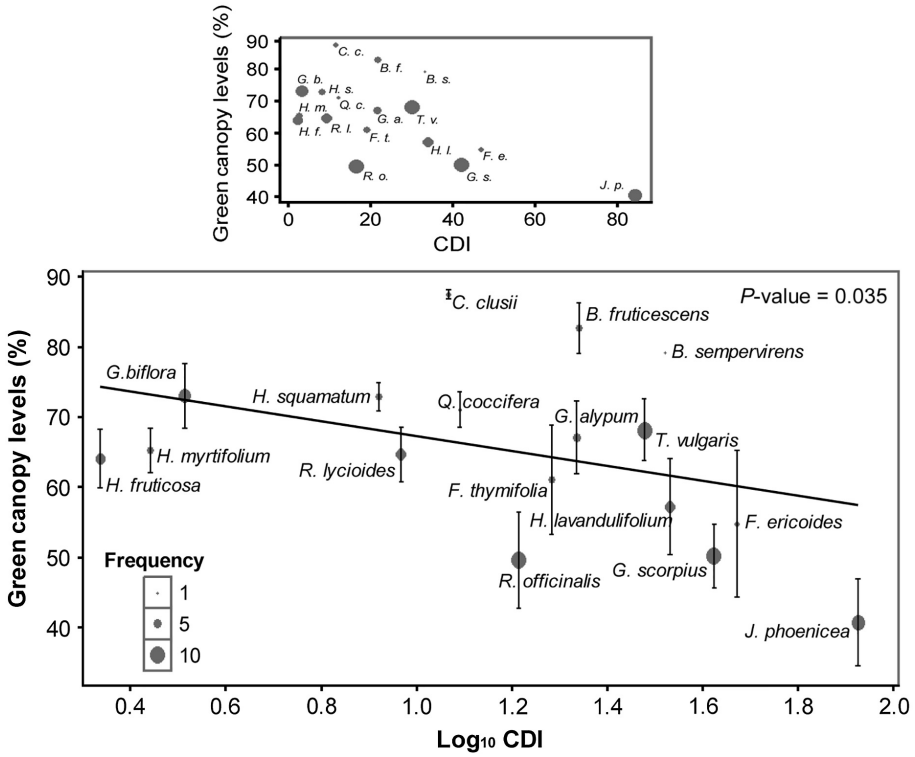

Fig. 5. Relationship between green canopy levels and Climatic Drought Index (CDI). Climatic Drought Index represents the ratio between the climatic suitability of the historic and extreme drought event periods (see text and Appendix S6). Climatic Drought Index values are logarithmically presented. The size of the dots represents the frequency of occurrence of each species across all sampling sites. Error bars represent standard errors. The figure above the main graph shows the same relationship between green canopy levels (vertical axis) and CDI (horizontal axis) without log-scaling CDI.

relationships in other biomes such as in the tropics, where strategies like leaf shedding might not be as common. Thus, logarithmic transformations should be explored after calculating CDI and not directly included in the formula.

Additionally, CDI is a ratio and it is sensitive to low values of climatic suitability during extreme drought events. Indeed, a variance partitioning analysis indicated that a 73% of the existing variation in CDI is explained by the climatic suitability of the extreme drought event, while only 8% of the variation is explained by historic climatic suitability. This analysis suggests that the extreme event suitability alone could be the main factor driving changes in green canopy. However, if historic climatic suitability and event climatic suitability are introduced into our models (both separately and as an interaction), they fail to explain changes in green canopy levels. Thus, the fact that CDI explains changes in canopy rather than each climatic suitability alone supports the idea that relative changes in climatic suitability drive changes in green canopy. At the same time, the degree to which a species perceives changes in climatic suitability is determined by both the historic conditions and the conditions experienced during the extreme event, with the latter ones having the biggest influence. Given the weight that the event climatic suitability has on CDI, high CDI values are more likely to be overestimated; thus, logarithmic transformations are again recommended after calculating CDI to reduce this effect. In turn, this ratio will highlight those species that show low climatic suitability during extreme drought events and therefore will likely be the most vulnerable species to drought based on our results. Calculations based on the difference in climatic suitability

between historic and extreme drought conditions could underestimate such species. Overall, our result suggests that species with traits or drought strategies leading to low CDI values and high green canopy levels could be better fit to drier environments. However, further research should be conducted on the demographic dynamics of populations experiencing high CDI values to assess whether high CDI values lead to demographic population decline.

The event caused obvious changes to the climatic suitability of the studied co-occurring species, irrespective of species' fit to previous climatic conditions. The fact that species historically living under more suitable climatic conditions failed to show greater resistance to an extreme drought event could be explained by the fact that species chronically subjected to suboptimal conditions can become acclimated (Gauthier and Jacobs 2011). Several studies have reported that trees that have previously experienced favorable conditions (i.e., that promoted growth) showed higher vulnerability to drought (McCulloh et al. 2012, Rowland et al. 2014). Alternatively, this pattern could be explained from a climatic niche perspective (Levins 1968, MacArthur 1984, Futuyma and Moreno 1988). Climate specialists can have narrow niche ranges and a high climatic suitability under optimal conditions, which rapidly declines as they move further from their climatic optima. On the other hand, climate generalists can have wide niche ranges with intermediate suitability levels across a wider range of climatic conditions. Based on the historic climatic suitability of each species and how it changed during the extreme drought event (Fig. 3), our community is mostly composed of climate specialists (e.g., *Helianthemum lavandulifolium*) with a few exceptions (e.g., *Genista biflora*). In a community dominated by climate specialists with similarly high historic suitability values, a potential relationship between historic suitability and green canopy levels would be lost due to the lack of variation in historic suitability. While climate specialists can be the most successful in relatively constant environments, climate generalists can outcompete climate specialists in future, more variable climates. Indeed, Buckley and Huey (2016) have shown that species tend to evolve wider niche ranges and intermediate performance levels in response to increased climatic variability. Thus, future climate scenarios can potentially shift this community to a climate generalist-dominated community either through climatic niche evolution of the existing species or through species replacement. The extent to which each one of these processes will dominate changes in the community will depend on the speed at which climate changes.

Our results did not support the hypothesis that abundant species would show a greater resistance to an extreme drought event. Green canopy levels were negatively related to species frequency (Fig. 4), indicating that species that are more represented in the area tend to have lower drought resistance relative to rare species. Life-history characteristics could explain this pattern. Frequent species such as *Rosmarinus officinalis* likely invest more resources in reproductive output and population density, at the cost of their ability to resist stressful conditions (according to an R-strategy). Moreover, a positive relationship between drought-induced mortality and subsequent seedling recruitment has been documented in Mediterranean shrublands of the region (Del Cacho and Lloret 2012). On the other hand, other species that exhibit traits closer to the K-strategy would enhance drought resistance by investing in reserves and physiological control of water use rather than reproduction (Muller-Landau 2010). This strategy would ultimately lead to lower recruitment density and less abundance across the landscape. Another explanation is that there could be selective pressure due to the drought conditions in the area. Populations of rare species with fewer individuals could experience stronger selection and adaptation than populations of frequent species, which likely exhibit more genetic flow (Vergeer et al. 2003). Low genetic flow in rare species together with strong selection pressures should lead to reduced variability in their green canopy levels compared to abundant species. Indeed, a linear regression between the standard deviation in green canopy levels and species frequency showed a positive relationship ($P = 0.008$, $R^2 = 0.41$), indicating that green canopy levels were less variable in rare species. This result also discards the possibility that the relationship found between green canopy levels and species frequency could be an artifact due to sampling bias. If this was the case, rare species should show higher variability in

green canopy levels than abundant ones. Overall, these results merit further exploration and interpretations need support from further research on the seed production, recruitment rates, and population genetics as well as testing using other SDM algorithms to assess their accuracy and reliability (Peterson et al. 2007).

Conclusions

We show that it is possible to interpret local processes at plant population level, such as drought-induced die-off, from the position of populations relative to their respective species climatic niche using SDMs. Our results especially highlight the functional relationship between species performance and changes in the climatic suitability of the area in which a species is found during extreme drought events. Therefore, this study demonstrates how vulnerable plant communities are to increasing climatic variability, a scenario likely to become ubiquitous in the future with climate change. In particular, extreme drought events are occurring globally (Allen et al. 2010, Greenwood et al. 2017), and here, we report drought effects in a Mediterranean shrubland, a type of ecosystem evolved under conditions of water deficit. These events could lead to community shifts (Lloret et al. 2012) and eventually the emergence of new communities that are more similar to those currently found in more arid regions (Ruiz-Labourdette et al. 2013). Such communities could be dominated by species that experience high suitability or low CDI values during extreme drought events. Species climatic niche estimated from SDMs can therefore be applied to describe responses to climatic disturbances—drought—using a CDI approach and, overall, picture the exposure and risk of species to climatic changes (Serra-Diaz et al. 2014).

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